

# REDESCRIPTION AND TAXONOMIC REAPPRAISAL OF *NEMERTOPSIS ACTINOPHILA* BÜRGER, 1904 (NEMERTEA: HOPLONEMERTEA: MONOSTILIFERA)

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## ABSTRACT

The anatomy of the monostiliferous hoplonemertean, *Nemertopsis actinophila* Bürger, 1904, is described in detail and illustrated for the first time. The systematic position of the species is reassessed and a new genus, *Cryptonemertes*, is established for it. I concluded on the basis of morphological and behavioral adaptations that the nemertean possesses an ectocommensal relationship with its actiniarian hosts.

*Nemertopsis actinophila* is an enigmatic species first described by Bürger (1904) from material collected by Römer and Schaudinn during their 1898 expedition to Spitzbergen and Kong Karls Land. Bürger's account of the morphology, though incomplete, records that the stomach opens into the rhynchodaeum immediately in front of the proboscis insertion without the intervention of an oesophagus, and that moderately developed dorsal fiber bundles (=accessory lateral nerves) occur in the longitudinal nerve cords. Friedrich (1955), in his synopsis of the monostiliferous hoplonemertean genera, stated that while *Nemertopsis actinophila* shared many characters with other species of *Nemertopsis*, he considered these two features to be fundamental differences sufficient to exclude *actinophila* from the genus. Friedrich concluded that the fusion of the two fiber bundles in each lateral nerve to form a single core further back approached the condition found in *Oerstediella*, but that the generic placement of Bürger's species would have to remain an open question. Subsequently, with the finding of additional specimens from Iceland, Friedrich (1958: 7) established "a new genus . . . *Nemertopsella*" for *actinophila*. This generic name, however, is preoccupied by *Nemertopsella* Wheeler (1940) for a species of Antarctic hoplonemertean, *N. marri* Wheeler; Friedrich (1955) unaccountably failed to include any reference to this genus in his synopsis, despite listing Wheeler's article in his bibliography. Although Gibson (1974) stated that Bürger's (1904) original name must for the time being at least be reinstated, he recently (Gibson, 1982a: 830) included both *actinophila* and *marri* in the genus *Nemertopsella* with the comment that because of differences in their internal organization "These 2 species probably belong to separate genera." The material described here enables a full description of the species and an assessment of its systematic position.

With the exception of two individuals found twisted among bryozoans, all of Bürger's (1904) specimens were obtained from beneath the pedal discs of the actiniarians *Tealia davisii*<sup>1</sup> (Agassiz) and *Stomphia polaris* (Danielssen). Bürger (1897-1907; 1904) concluded that because the color of the nemerteans always exactly matched that of the actiniarians with which they were associated, *Nemertopsis actinophila* (1904: 58) "handelt sich im vorliegenden Falle wohl lediglich um einen Raumparasitismus." The species has subsequently often been cited in the literature as a commensal (Hyman, 1951; Gontcharoff, 1961; Cheng, 1964;

<sup>1</sup> O. Carlgren identified the anemones referred to by Bürger (1904). *Tealia davisii* is no longer recognized as a valid taxon and the identity of this host thus remains uncertain. Manuel (1981) notes that the generic name *Urticina* Ehrenberg has priority over the better-known name *Tealia* Gosse.

Noble and Noble, 1971) yet, as Gibson (1972) pointed out, in most instances relating to parasitic or commensal habits in nemerteans the relationship between the worms and their hosts is not clearly understood. To suggest that a species is a commensal merely because its color matches that of an organism with which it appears to be associated is premature; some evidence of morphological, physiological, ecological or behavioral adaptation must be demonstrated before such a conclusion can be substantiated. Whether or not *Nemertopsis actinophila* enjoys a commensal relationship with actiniarian hosts thus remains open to speculation.

### MATERIALS AND METHODS

The three specimens of *Nemertopsis actinophila* upon which the present redescription is based were found beneath the pedal discs of two species of swimming actiniarians. Two came from specimens of *Stomphia coccinea* (O. F. Müller) obtained by Dr. E. Robson in the vicinity of Friday Harbor, San Juan Island, Puget Sound (48°32'N, 123°00'W), during September 1959 and September 1963, the third from *Stomphia didemon* Siebert collected by Dr. P. Illg from Satellite Channel, off Vancouver Island (48°43'N, 123°30'W), during September 1963. The nemerteans were anaesthetized by adding isotonic MgCl<sub>2</sub> to seawater prior to fixation in Susa's fluid and storage in methyl benzoate. They have been sectioned at 6–7  $\mu$ m in 56°C melting point wax and stained by the Mallory trichrome method. The material is deposited at the British Museum (Natural History), London, under Registration Numbers 1984.10.23–1984.10.25.

Accounts of the nemerteans' behavior and appearance in life are based upon observations made by Dr. E. Robson, University of Reading, supplemented by information contained in a Christmas card produced by Dr. G. Thorson in December 1949.

### *Nemertopsis actinophila* Bürger, 1904

*Nemertopsis actinophila* Bürger, 1897–1907, pp. 425, 528; 1904, pp. 58, 59, pl. 3, figs. 1, 5–8; Böhmig, 1929, p. 91; Coe, 1944, p. 60; Hyman, 1951, pp. 492, 498, 520, fig. 195F; Gontcharoff, 1961, pp. 863, 872; Gibson, 1972, pp. 80, 182; 1974, pp. 247, 248, 250–253, 255–264.

*Nemertopsella actinophila* (Bürger) Friedrich, 1958, pp. 6–8, 22, 23; Gibson, 1974, p. 247; 1982a, p. 829.

(General invertebrate or parasitology texts referring to the species are excluded from the above list of references.)

**External Appearance.**—In life the nemerteans were up to 40 mm long and about 1 mm wide when extended, 15 mm long and 1.5 mm wide when contracted; Bürger (1904) recorded lengths of 15–45 mm and widths of 1.5–2 mm. The oval head (Fig. 1) bears four eyes and extremely shallow lateral furrows, whose cilia create posteriorly-directed currents. The two anterior eyes are distinct, but the posterior and smaller pair is often masked by cephalic coloration. Behind the head the elongate slender body gradually tapers to end in a bluntly rounded tail. The general appearance of one of the individuals found with *Stomphia coccinea*, in normal extension and fully contracted, is illustrated in Figure 2.

Bürger (1904: 58) stated that in life *Nemertopsis actinophila* is bright red, red-orange, red-yellow or red-brown, the color always exactly conforming with that of their actiniarian hosts. The present specimens were a general orange or orange-red hue, similar to that of the *Stomphia* species with which they were found; Robson's laboratory notes record that the nemerteans possessed an "Orange-red colouration, i.e., general orange background with very clear red sinuous blood vessel down back: whitish portions between correspond to internal structures . . . epidermis relatively colourless." The color of *Nemertopsis actinophila* is at least partly due to scarlet pigment contained in blood corpuscles; blood vessels are very obvious in living worms (Fig. 3) and are contractile.

**Body Wall, Musculature and Parenchyma.**—The epidermis, up to about 75  $\mu$ m in maximum thickness, contains enormous numbers of slender acidophilic glands

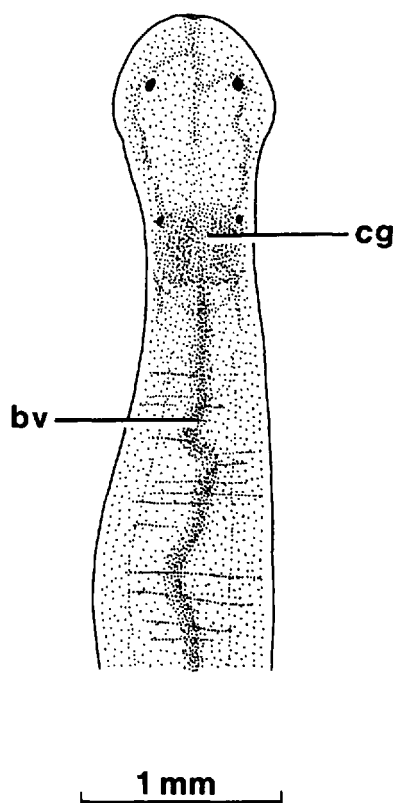
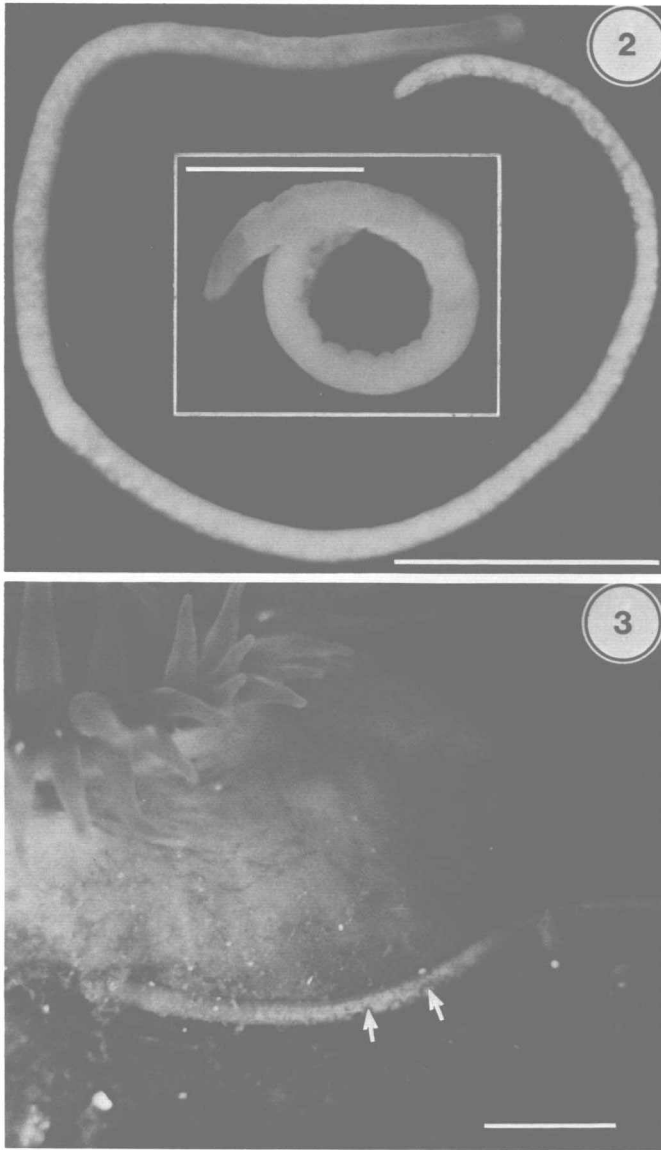


Figure 1. *Cryptonemertes actinophila*. Drawing to show the external appearance of the anterior end of a living specimen, based on a sketch by Dr. E. Robson. One of the dorsolateral blood vessels (bv) is twisted around to a median position above the rhynchocoel; the darker coloration of the blood vessels and cerebral ganglionic region is due to the pigment contained within the blood corpuscles: see text for further detail. cg, cerebral ganglia.

(Fig. 4). Beneath the connective tissue dermis, 7–12  $\mu\text{m}$  thick, outer circular and inner longitudinal body wall muscle layers are respectively 7–15  $\mu\text{m}$  and 30–60  $\mu\text{m}$  deep. The relative dimensions of these body wall layers closely agree with Bürger's (1904: 58, pl. 3, figs. 5–8) account and illustrations.

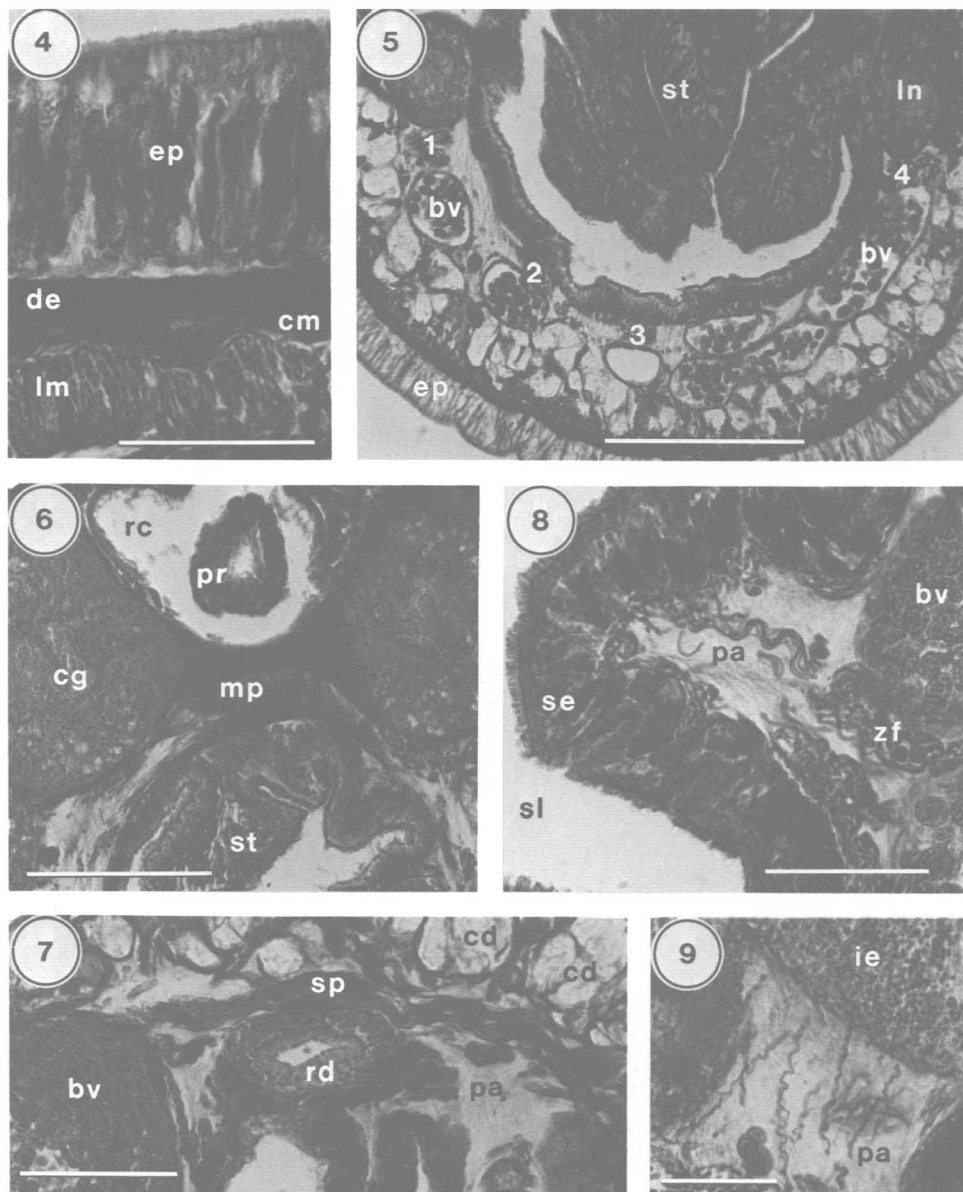
In anterior foregut region four bundles of muscle fibers separate from longitudinal musculature and extend forwards in parenchyma (Fig. 5). One bundle runs immediately below each lateral nerve cord, continues anteriorly below brain lobes and then turns inwards just in front of ventral cerebral commissure to form plate of transverse musculature passing between foregut and rhynchocoel (Fig. 6); isolated dorsoventral muscles extending from ventrolateral body margins also contribute to this muscle plate. The two other longitudinal muscle bundles run below the foregut, gradually moving laterally before they too join the transverse muscle band. Dorsally and dorsolaterally cephalic gland lobules in vicinity of brain incompletely divide longitudinal muscle layer into inner and outer portions; fibers of inner zone lead to proboscis insertion. There is no pre-cerebral septum, as defined by Kirsteuer (1974), but bundles of muscle fibers derived from body wall longitudinal layer lead to well-developed supra-rhynchodaeal transverse muscle plate (Fig. 7) in front of proboscis insertion. In the head loosely disposed bundles of oblique, radial and dorsoventral muscle fibers pass irregularly between



Figures 2 and 3. *Cryptonemertes actinophila*. 2. Photograph of the living specimen found under *Stomphia didemon* when extended with Inset, the same individual fully contracted. Scales = 5 mm. 3. Photograph of a specimen emerging from beneath the base of a *Stomphia coccinea* under which it had been living. Note the blood vessels showing through the body wall of the nemertean (arrowed). Scale = 5 mm. Both Figures taken from color transparencies by Dr. E. Robson.

blood vessels and cephalic glands to form cephalic retractor muscle network which, in tip of head, largely replaces body wall longitudinal muscle layer.

Unlike many hoplonemerteans, there are no dorsoventral muscles in intestinal region, but throughout length of gut "zigzag" fibers radiate inwards through parenchyma. Around the foregut these fibers may be grouped to form well developed muscle bundles (Fig. 8), whereas in intestinal region the fibers are usually isolated



Figures 4-9. *Crytonemertes actinophila*. 4. Transverse section through part of the body wall. cm, body wall circular muscle layer; de, dermis; ep, epidermis; lm, body wall longitudinal muscle layer. Mallory. Scale = 50  $\mu$ m. 5. Transverse section through the post-cerebral region to show the four bundles of longitudinal muscle fibers (1-4) which lead forwards to form the transverse muscle plate over the foregut. bv, blood vessel; ep, epidermis; ln, lateral nerve cord; st, stomach. Mallory. Scale = 200  $\mu$ m. 6. Transverse section through the posterior cerebral region to show the muscle plate (mp) between the rhynchocoel (rc) and anterior portion of the stomach (st). cg, cerebral ganglion; pr, proboscis. Mallory. Scale = 150  $\mu$ m. 7. Transverse section to show the posterior portion of the rhynchodaeum (rd) and supra-rhynchodaeal muscle plate (sp). bv, blood vessel; cd, cephalic gland lobule; pa, parenchyma. Mallory. Scale = 100  $\mu$ m. 8. Part of the stomach region in transverse section to show the bundles of radial "zigzag" muscle fibers (zf). bv, blood vessel; pa, parenchyma; se, stomach epithelium; sl, stomach lumen. Mallory. Scale = 50  $\mu$ m. 9. A part of the intestinal region in transverse section to show the isolated nature of the "zigzag" fibers. ie, intestinal epithelium; pa, parenchyma. Mallory. Scale = 50  $\mu$ m.

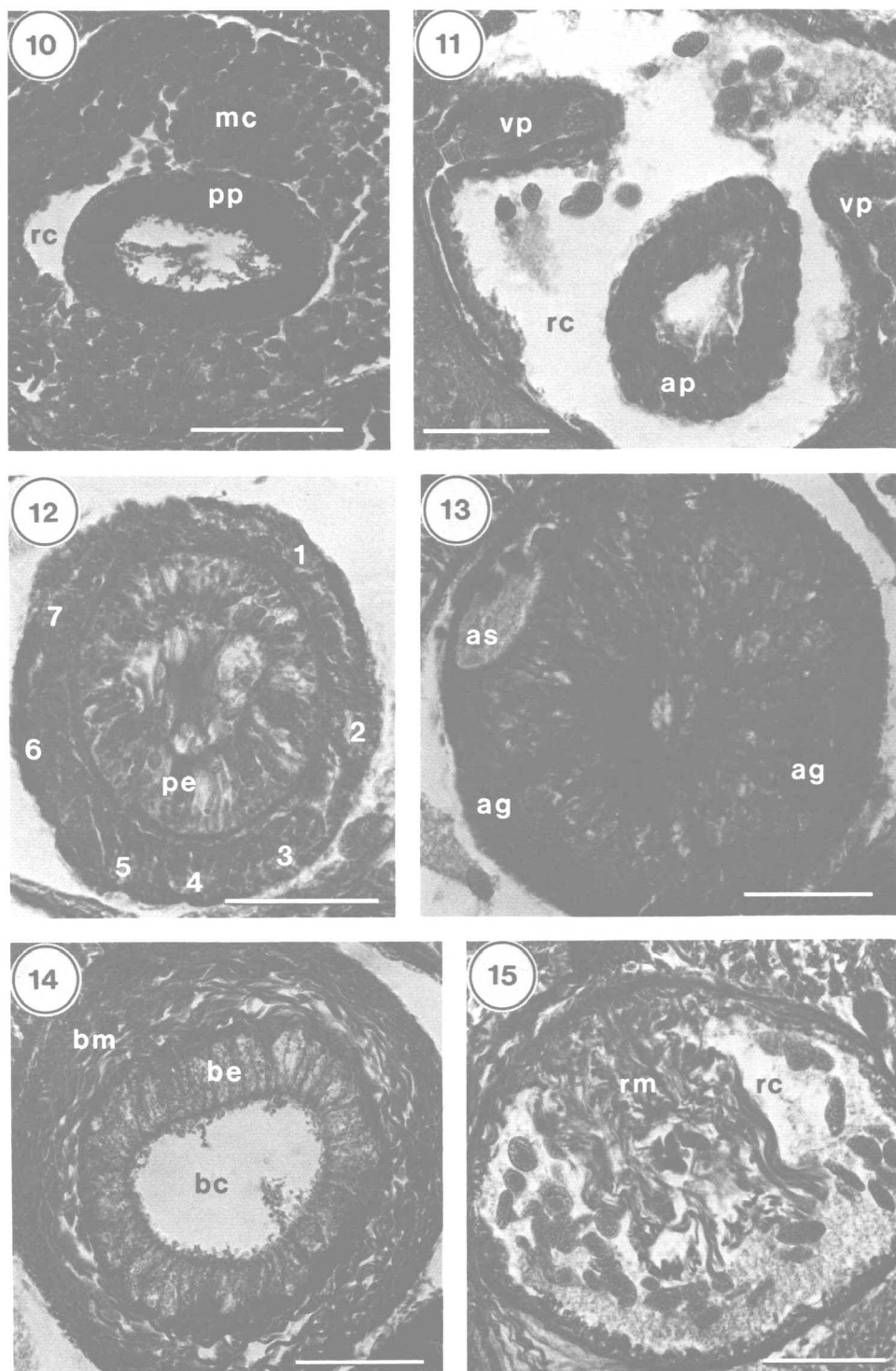
(Fig. 9); it is possible that the zigzag appearance is a consequence of exposure to magnesium ions prior to fixation (Robson, pers. comm.). Parenchymatous connective tissues moderately extensive, particularly in anterior regions where they surround foregut, rhynchocoel and branches of blood system.

*Proboscis Apparatus.*—The rhynchodaeum opens subterminally from short median ventral groove at tip of head. For most of its length the rhynchodaeum comprises a thin-walled (6–8  $\mu\text{m}$ ) chamber, its epithelium neither ciliated nor glandular. Occasional longitudinal or circular muscle fibers adjacent to epithelium appear derived from general cephalic musculature rather than forming specific muscle layer. Posteriorly, however, the rhynchodaeum becomes restricted to slender dorsal tube (Fig. 7), lined by thicker epithelium (15–20  $\mu\text{m}$ ) and enclosed by well developed layer of interwoven longitudinal and circular muscle fibers; this region, about 50  $\mu\text{m}$  long, ends at proboscis insertion.

The rhynchocoel is short, 15–25% of body length. For most of its length it is extremely thin walled, its endothelium, longitudinal and circular muscles together being at most 5–8  $\mu\text{m}$  across. Posteriorly, however, the muscle layers are better developed and each may be 5–6  $\mu\text{m}$  thick. The rhynchocoel varies between 20–35% of body diameter, often being locally dilated by dense accumulations of mononucleate cells histologically identical to blood corpuscles (Fig. 10). Many parts of chamber also contain a finely particulate and homogeneous “fluid” similar to blood plasma.

The proboscis, described by Bürger (1904: 58) as strongly developed for size of species, comprises four distinct regions. The most anterior portion, leading from proboscis insertion, is simple tubular structure 90–100  $\mu\text{m}$  in diameter composed of longitudinal muscle fibers lined externally by non-glandular epithelium (Fig. 11). Indistinct traces of proboscis nerve supply can just be discerned between muscle fibers. As it extends posteriorly, proboscis gradually becomes wider and differentiated into main anterior chamber (Fig. 12). This comprises glandular epithelium 15–25  $\mu\text{m}$  thick lined by thin but distinct connective tissue basement membrane, delicate circular muscle layer 3–6  $\mu\text{m}$  across, longitudinal coat up to about 25  $\mu\text{m}$  in maximum width containing seven irregularly distributed proboscis nerves, inner layer of circular muscles only one or two fibers thick, and extremely thin lining endothelium. The anterior chamber has an overall diameter of about 130–150  $\mu\text{m}$ . There is no clear delimitation between anterior chamber and extreme anterior portion of proboscis.

The third region, the stylet bulb, is the widest part of proboscis and attains maximum diameter of 190–195  $\mu\text{m}$ . The front part is characterized by peripheral ring of coarsely granular acidophilic glands (Fig. 13), penetrated by posterior extensions of proboscis nerve supply, which are then replaced further back by basophilic glandular lobules. The accessory stylet pouches, each containing up to eight accessory stylets in various stages of styletogenesis, are situated at interface between the two gland types (Fig. 13). Two of the specimens possess four accessory stylet pouches, the third only two. The thin epithelium lining lumen of this region is surrounded by sphincter of radial muscle fibers which turn posteriorly and lead to muscle bulb enclosing stylet basis. Cylindrical basis is about 30  $\mu\text{m}$  in diameter and 40–45  $\mu\text{m}$  long. The central stylet of each specimen has been lost, but the organic matrix core of larger accessory stylets is up to about 25  $\mu\text{m}$  long, suggesting intact stylet length of about 40–45  $\mu\text{m}$ , i.e., stylet to basis ratio approximates 1:1; this agrees with Bürger's (1904) findings. Stricker (1983: 154) stated that, except for occasional surface wear, “the structure of the central stylet was found to be identical to that of a mature reserve stylet in a given species.” Behind basis the



Figures 10–15. *Cryptonemertes actinophila*. 10. Transverse section through a part of the rhynchocoel (rc) distended by enormous numbers of mononucleate blood corpuscles (mc). pp, posterior portion of proboscis. Mallory. Scale = 100  $\mu$ m. 11. Transverse section through the cerebral region to show

muscle bulb contains spacious central chamber, lined by glandular epithelium 15–30  $\mu\text{m}$  thick, enclosed by well developed band of interwoven circular and longitudinal muscle fibers (Fig. 14). At rear of bulb region the chamber is reduced to slender median duct and muscle band is up to 75  $\mu\text{m}$  thick.

The posterior proboscis chamber, accounting for approximately 60% of total proboscis length, is lined by strongly acidophilic glandular epithelium, 40–45  $\mu\text{m}$  thick, enclosed by slender outer longitudinal and inner circular muscle coats and delicate endothelium (Fig. 10). The strong proboscis retractor muscle (Fig. 15) is attached to dorsal wall of rhynchocoel approximately 1 mm before chamber ends.

*Alimentary Canal.*—The foregut opens into rhynchodaeum immediately in front of proboscis insertion. It is evident from the present specimens that the position of the stomach is extremely variable and that the foregut is regionally differentiated. Most of foregut is typically hoplonemertean in form, its epithelium containing large numbers of basophilic and acidophilic gland cells (Fig. 16), but an anterior portion is recognizable in which there are few acidophils and no basophils (Fig. 17). A further feature distinguishing the two regions is the well developed longitudinal splanchnic muscle layer, 6–12  $\mu\text{m}$  thick, which invests anterior portion of foregut. These splanchnic fibers are situated between epithelium and connective tissue sheath which encloses foregut as a whole. It appears to be degree of contraction or elongation of muscular anterior foregut region which determines position of stomach. In one specimen stomach is located far behind cerebral ganglia, the anterior foregut then appearing as long narrow channel with characteristic 'oesophageal' appearance (Fig. 18), in another the anterior portion is strongly contracted and much of stomach is pulled forward to pre-cerebral position, and in the third individual an intermediate condition exists with stomach extending back from between brain lobes. Whether the anterior muscular part of foregut should be termed an oesophagus or be regarded as a specialized portion of stomach is arguable; in other hoplonemerteans with a stomach similarly divisible into two regions (Moore and Gibson, 1981; Gibson, 1982b), an oesophageal region is also distinguishable on histological grounds.

Posteriorly the stomach becomes narrower, its epithelium remaining folded but containing fewer gland cells. This region, overlying the intestinal caecum, constitutes the pyloric portion of foregut which opens into dorsal intestinal wall (Fig. 19).

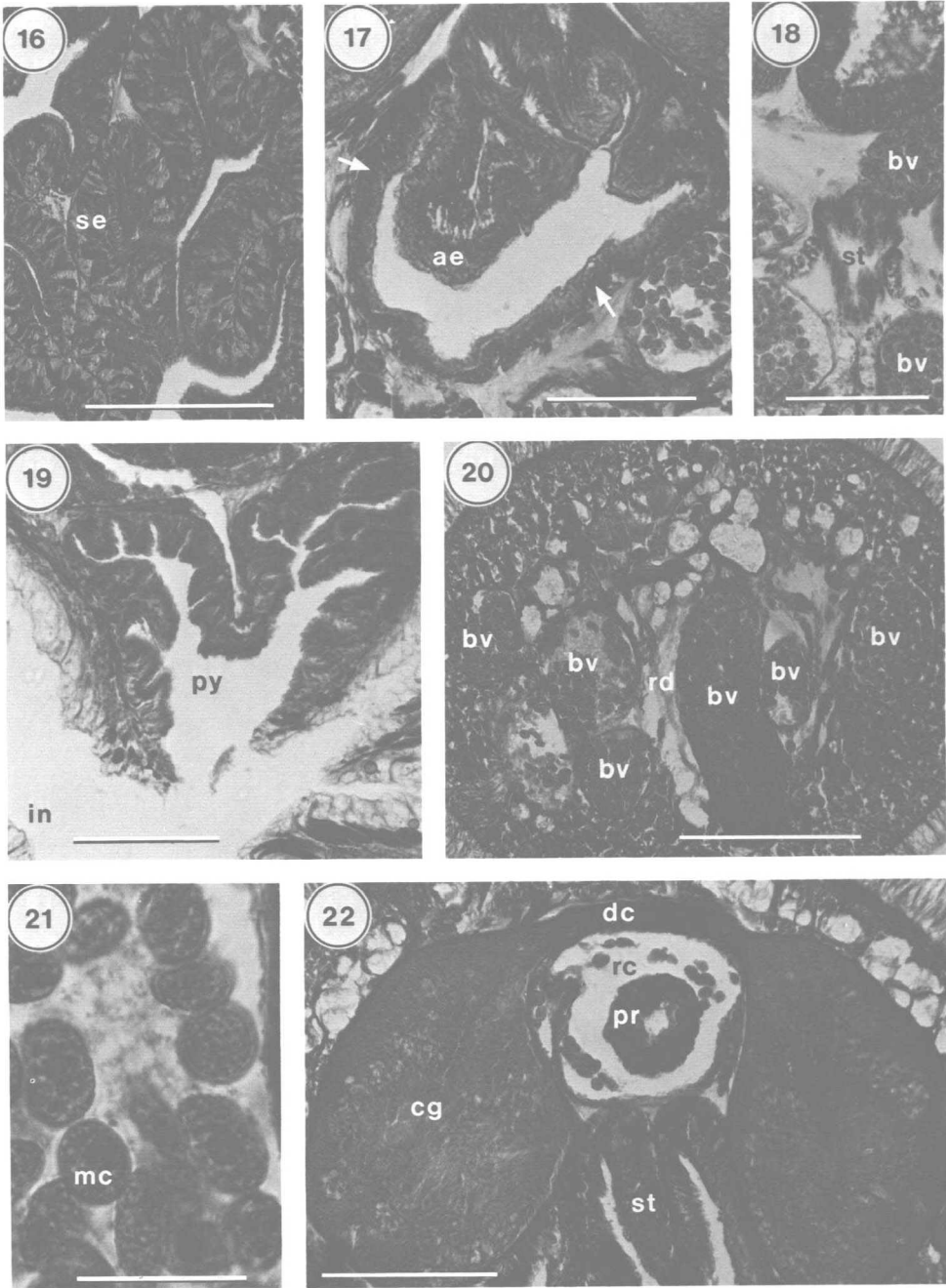
The intestinal caecum reaches forwards to about mid-stomach level and possesses lateral but no anterior pouches. For the remainder of its length the intestine, which possesses a normal hoplonemertean construction, bears unbranched lateral diverticula.

*Blood System.*—The blood system is complex, extremely well developed (Fig. 3) and unusual in its arrangement. All vessels are large and possess circular muscle fibers in their thick walls. The cephalic supply consists of single spacious median

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the extreme anterior portion of the proboscis (ap) and the two vascular plugs (vp). rc, rhynchocoel. Mallory. Scale = 50  $\mu\text{m}$ . 12. Transverse section to show the structure of the main anterior region of the proboscis. pe, proboscis epithelium; 1–7, proboscis nerves. Mallory. Scale = 50  $\mu\text{m}$ . 13. Transverse section through the stylet bulb region of the proboscis at the level of the accessory stylet pouches (as). ag, acidophilic glands. Mallory. Scale = 50  $\mu\text{m}$ . 14. Transverse section through the muscular bulb region of the central proboscis to show the spacious central chamber (bc) surrounded by a meshwork of interwoven circular and longitudinal muscle fibers (bm). be, bulb epithelium. Mallory. Scale = 50  $\mu\text{m}$ . 15. Transverse section through the posterior region of the rhynchocoel (rc) to show the dorsal attachment of the powerful proboscis retractor muscle (rm). Mallory. Scale = 50  $\mu\text{m}$ .





Figures 16–22. *Cryptonemertes actinophila*. 16. Part of the posterior stomach region in transverse section to show the construction of its epithelium (se). Mallory. Scale = 200  $\mu$ m. 17. Transverse section through the anterior stomach region. Arrows indicate the longitudinal splanchnic muscle layer. ae, epithelium of anterior stomach region. Mallory. Scale = 100  $\mu$ m. 18. Transverse section through the anterior stomach region (st) of a specimen in which this portion of the foregut is stretched to the extent that it looks like an "oesophagus." The splanchnic muscle fibers appear dark at the base of the epithelium. bv, blood vessel. Mallory. Scale = 100  $\mu$ m. 19. Transverse section to show the junction between the pyloric region of the foregut (py) and intestine (in). Mallory. Scale = 100  $\mu$ m. 20. Transverse

terminal lacuna, approximately one-third width of head, which branches to form complex of large, irregularly arranged and interconnected vessels running alongside rhynchodaeum (Fig. 20). At front of brain the most dorsal cephalic vessel on each side of head moves to position immediately adjacent to rhynchocoel wall, through which it then bulges to form large vascular plug (Fig. 11); the two plugs are located in front of dorsal cerebral commissure. Behind the vascular plugs each vessel then emerges from rhynchocoel wall to run between it and cerebral ganglia and then, behind brain, moves to dorsolateral position next to body wall muscles where it joins post-cerebral plexus. A particularly unusual characteristic of the blood system is that it lacks typical hoplonemertean mid-dorsal vessel running below rhynchocoel. The remaining cephalic vessels continue posteriorly, passing below stomach and brain lobes, to contribute to post-cerebral blood supply. This consists of peripheral plexus of spacious vessels running in parenchyma between gut and body wall. The network of vessels extends remaining length of body but tends to be less complex in posterior half. The plan of the blood system thus closely conforms to that reported by Bürger (1904) and Friedrich (1958).

Friedrich (1958: 7–8) commented that the blood vessels “are filled with small rounded corpuscles. It could not be decided whether these corpuscles are blood cells or the product of coagulation.” In most parts of the body the blood vessels of the present nemerteans are packed with enormous numbers of spherical to oval, acidophilic and coarsely granular mononucleate cells, up to about 18  $\mu\text{m}$  in maximum diameter (Fig. 21); histologically identical corpuscles occur in the rhynchocoel. The corpuscles in life are uniformly scarlet, although a few contain black granules (Robson’s notes, May 1960); this pigmentation may be due to haemoglobin.

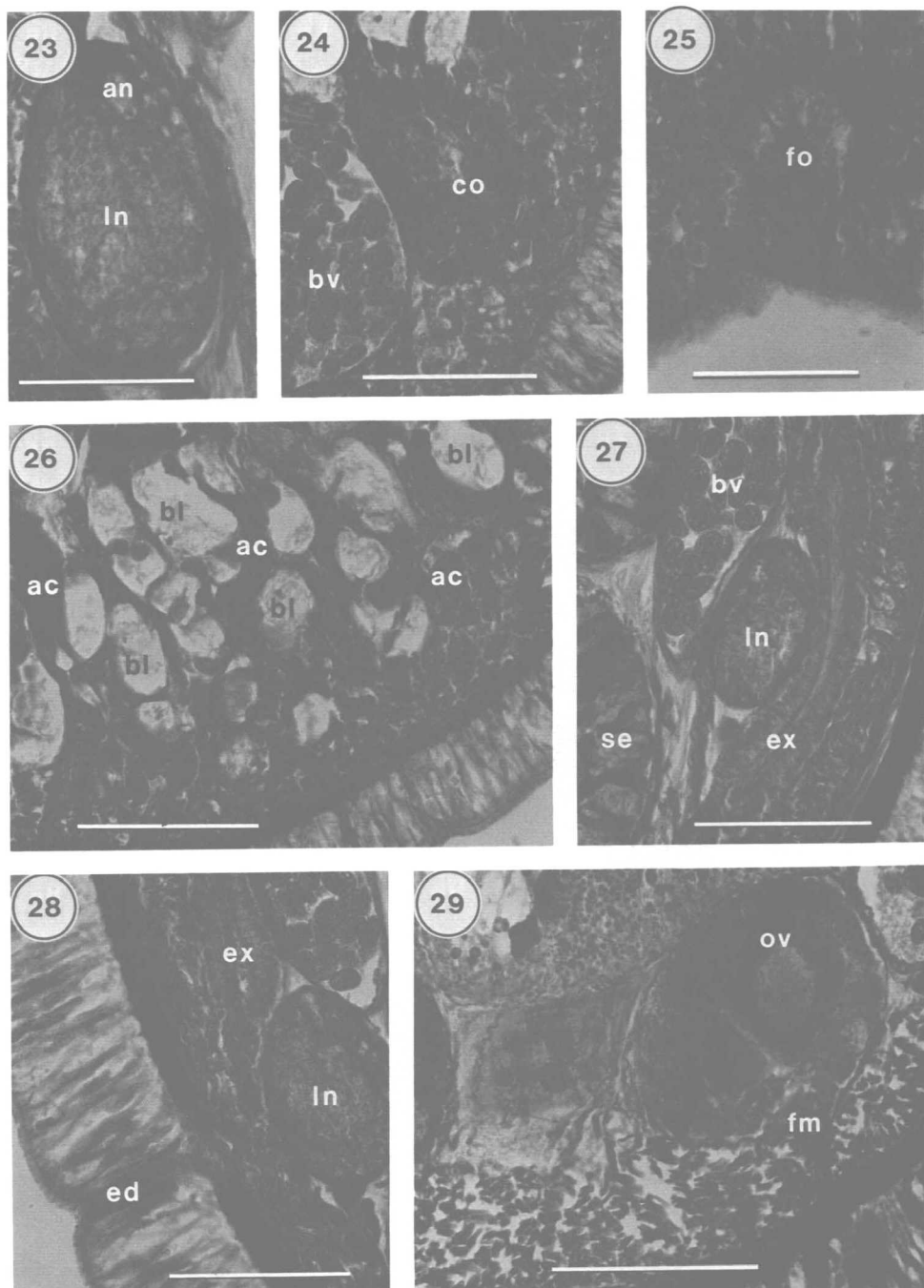
Robson also recorded observations on blood circulation. She noted (September 1959) that blood vessels are contractile, the blood being moved by peristaltic waves of irregular frequency; 11 waves were counted in 5 min at a temperature of 20°C. The direction of circulation is generally forwards in the dorsal vessels and backwards in the ventral, although it may be reversed, especially when the animal’s head moves. The circulation is stopped by 15 minutes immersion in a muscle anaesthetic (3:1 seawater : 7.5%  $\text{MgCl}_2$ ).

*Nervous System.*—The cerebral ganglia (Fig. 22) are compact and confined to dorsal half of head. They are enclosed by distinct connective tissue outer neurilemma, but fibrous and neuropil tissues are in direct contact with no inner neurilemma. The ventral cerebral commissure is short and 35–40  $\mu\text{m}$  wide whereas dorsal commissure, located posterior to ventral, arches over rhynchocoel and is at most about 20  $\mu\text{m}$  across. Bürger’s (1904: 58) comment that the ventral commissure is attenuated evidently refers to a distorted individual, illustrated in his pl. 3, fig. 5, in which the stomach is pulled well forward.

The lateral nerve cords, as noted by Bürger (1904) and Friedrich (1958), each contain a dorsal fibre bundle (accessory lateral nerve) (Fig. 23) derived from the dorsal ganglionic lobes. The accessory nerves, at most about 15  $\mu\text{m}$  in diameter, can be traced back to the anterior intestinal regions where they fuse with the main

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section through the cephalic region to show the well developed blood supply. bv, blood vessel; rd, rhynchodaeum. Mallory. Scale = 200  $\mu\text{m}$ . 21. Oil immersion photomicrograph to show the appearance of the mononucleate blood corpuscles (mc). Mallory. Scale = 25  $\mu\text{m}$ . 22. Transverse section through the cerebral ganglia (cg) at the level of the dorsal cerebral commissure (dc). pr, proboscis; rc, rhynchocoel; st, stomach. Mallory. Scale = 150  $\mu\text{m}$ .



Figures 23–29. *Crytonemertes actinophila*. 23. Transverse section through the anterior region of a lateral nerve cord (ln) to show the accessory lateral nerve (an). Mallory. Scale = 50  $\mu$ m. 24. Transverse section to show the simple construction of a cerebral sensory organ (co). bv, blood vessel. Mallory. Scale = 75  $\mu$ m. 25. Transverse section to show the appearance of the frontal organ (fo). Mallory. Scale = 50  $\mu$ m. 26. Part of the ventral cephalic region in transverse section to show the two types of cephalic glands. ac, acidophilic cephalic gland; bl, basophilic cephalic gland lobule. Mallory. Scale = 75  $\mu$ m. 27. Transverse section through part of the foregut region to show an excretory collecting tubule

fibrous tissues of the lateral cords. For the remaining body length the lateral nerves contain a single fibre core.

Several major cephalic nerves can be distinguished, extending forwards alongside rhynchodaeum or running dorsolaterally near extreme anterior portion of rhynchocoel. One of the dorsolateral nerves on each side enters proboscis insertion and contributes to innervation of organ. Other nerves emerging from brain lobes supply eyes, cerebral sensory organs and cephalic glands. The general peripheral nervous system is supplemented by branches leading at irregular intervals from lateral nerve cords.

*Cerebral Sensory Organs.* Although Friedrich (1958: 7) stated that "No cerebral organ could be detected," Bürger (1904: 58) said that they were small spherical structures situated far in front of the brain below the cephalic blood vessels. In the present specimens the cerebral organs are situated ventrolaterally well in front of brain. They are simple, oval sac-like structures (Fig. 24), about 90  $\mu\text{m}$  in maximum dimension, opening from exterior via short, slender ciliated canals and essentially consisting of a ciliated chamber surrounded by neural and glandular tissues.

*Ocelli.*—*Nemertopsis actinophila* possesses four eyes. The two anterior eyes are simple pigment cup ocelli up to about 30  $\mu\text{m}$  in diameter, situated amongst cephalic glands near tip of head. In contrast, the posterior eyes consist only of irregular aggregations of pigment granules located alongside the cerebral ganglia; their appearance is quite variable.

*Frontal Organ and Cephalic Glands.*—Although Bürger (1904: 58) described, but did not illustrate, a strongly developed head pit, the frontal organ of the present specimens (Fig. 25) is small, 35–40  $\mu\text{m}$  in diameter, and opens near tip of head. The extensive development of cephalic glands, however, conforms with Bürger's (1904) description. Two types of glands are distinguishable (Fig. 26), large basophilic lobules with foamy contents, interspersed between which are small and irregularly shaped acidophilic granular gland cells. The glands fill much of the cephalic space in tip of head but otherwise form an irregular peripheral layer just below body wall musculature. Both types extend behind brain into anterior third of stomach region where they displace fibers of longitudinal muscle layer. On ventral margins acidophilic glands reach rather more posteriorly, to about mid-stomach level, where they are scattered in a submuscular position.

*Excretory System.*—The excretory system is restricted to stomach region, anterior to intestinal caecum. Main collecting tubules are thick-walled (10–12  $\mu\text{m}$ ) with overall diameter of about 30–35  $\mu\text{m}$ , strongly ciliated and possess typical histological appearance. They run mainly close or immediately adjacent to lateral nerve cords (Fig. 27), but may reach more dorsolaterally near branches of blood system. A single small nephridiopore opens laterally on each side close to nerve cords (Fig. 28); the arrangement agrees closely with Bürger's (1904) description. No trace of flame cells could be distinguished in any part of excretory system.

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(ex) running between a lateral nerve cord (ln) and the body wall. bv, blood vessel; se, stomach epithelium. Mallory. Scale = 75  $\mu\text{m}$ . 28. Transverse section to show a nephridiopore opening adjacent to a lateral nerve cord (ln). ed, efferent duct of excretory system; ex, excretory collecting tubule. Mallory. Scale = 75  $\mu\text{m}$ . 29. Transverse section through a gonad to show well formed ova (ov) and the distal accumulation of "filamentous" material (fm) which appears to represent spermatozoa. Mallory. Scale = 100  $\mu\text{m}$ .

*Reproductive System.* — Bürger (1904: 58), who evidently examined only one specimen histologically, stated that *Nemertopsis actinophila* was probably dioecious. Evidence from one of the present specimens, however, suggests that the species is hermaphroditic. Gonads are very numerous and irregularly distributed on all sides of body, even extending to mid-dorsal position behind rhynchocoel. Most of gonads exhibit unusual appearance in that developing ova, with nuclei 35–40  $\mu\text{m}$  in diameter containing several nucleolar bodies, are confined to their proximal portions, whilst distal region (adjacent to body wall musculature) consists of differently staining tissues arranged around unopened gonoduct plugged with mass of “filamentous” material resembling sperm tails (Fig. 29). Undifferentiated gonads in the two sexually immature specimens also commonly possess a distal duct partially protruding into body wall muscle layers. This arrangement suggests that *Nemertopsis actinophila* may be a protandrous hermaphrodite, with ova and sperm produced within the same gonads. Oviparity remains probable but unconfirmed; few hoplonemertean taxa are known to be ovoviviparous (Gibson, 1972).

#### SYSTEMATIC DISCUSSION

Although Bürger's (1904) description of *Nemertopsis actinophila*, supported by his illustrations, is far from complete, it does include information on several important anatomical features; of particular significance are the organization of the blood, nervous and reproductive systems. The anatomy of these systems in the present specimens is in accordance with Bürger's account, but close similarities are also evident in the arrangement of the alimentary tract, proboscis apparatus, body wall and cephalic glands. Those differences which are apparent, such as the number of accessory stylet pouches in the proboscis, are not considered to be more than examples of intraspecific variation. Since the external features of the present nemerteans also conform with Bürger's material and the worms were found in an identical location below the pedal disc of actiniarians, they are identified as *Nemertopsis actinophila*.

Friedrich (1955) excluded *actinophila* from the genus *Nemertopsis* for two reasons, because of the way in which the foregut opened into the rhynchodaeum and because of the presence of an accessory lateral nerve in the anterior regions of the lateral nerve cords. The genus *Nemertopsis*, with four species and one subspecies (Gibson, 1982a), is not securely diagnosed, but studies of the present specimens reveal anatomical characteristics in addition to those specified by Friedrich (1955) which differ from features reported for other *Nemertopsis* species. Thus in contrast to the condition found in *actinophila*, *Nemertopsis* species possess a simple blood system with a single mid-dorsal vessel running between the rhynchocoel and gut, are dioecious with their gonads distributed in the primitive lateral position between the intestinal diverticula, and possess a distinct oesophagus (Wheeler, 1934; Corrêa, 1955; Friedrich, 1955; Brunberg, 1964; Gibson, 1982c). In at least two species, including the type species *Nemertopsis bivittata* (Delle Chiaje), there is a pre-cerebral septum (Corrêa, 1955; Brunberg, 1964), whereas none is found in *actinophila*. How significant are these differences? Recent studies by Moore and Gibson (1981) and Gibson et al. (1982) have shown that in terrestrial nemerteans of the genera *Antiponemertes* and *Pantinonemertes* the presence or absence of an accessory lateral nerve varies interspecifically. Similarly, whether or not the foregut possesses an oesophageal region depends upon the species concerned in the freshwater genus *Prostoma* (Gibson and Moore, 1976). The value of these features as generic characters in marine hoplonemerteans is thus open to question. However, the complex organization of the blood system in *actinophila* is very different from

that of any other hoplonemertean and, though later (p. 57) related to the species' adoption of commensal habits, must be regarded as a major character. Gonad multiplication, also considered to be a consequence of commensalism, is by itself not necessarily of generic significance but in combination with hermaphroditism differs strikingly from the normal *Nemertopsis* arrangement. The absence of a pre-cerebral septum, which Kirsteuer (1974) included as a generic feature, also contrasts markedly with at least two species of *Nemertopsis*. It is concluded that what must be evaluated is not the importance of individual features but the significance of the total combination of characters, and on this basis *actinophila* cannot be retained within the genus *Nemertopsis*.

As indicated earlier, Friedrich (1958) employed a previously used and currently valid name in transferring *actinophila* to the "new" genus *Nemertopsella*. Wheeler's species, *Nemertopsella marri*, differs from *actinophila* in possessing a distinct oesophagus, a much longer rhynchocoel, no accessory lateral nerves and several eyes arranged in four groups; more significantly its blood system, as shown in Wheeler's (1940: fig. 14) diagrams, is of a much simpler plan. This combination of characters indicates that *actinophila* does not belong in the genus *Nemertopsella* sensu Wheeler (1940).

In the earlier sections of his key to the monostiliferous hoplonemertean genera, Friedrich (1955) includes the following characters: mouth and proboscis pore separate or united; rhynchocoel wall musculature consisting of two separate layers or a single layer of interwoven circular and longitudinal fibers; lateral nerve cords with or without accessory lateral nerves; rhynchocoel short (less than about one-third of the body length) or as long as the body. The present specimens, apart from possessing accessory lateral nerves whose generic significance is now debatable, have their mouth and proboscis pore opening via a common aperture and a rhynchocoel less than half the body length containing separate longitudinal and circular muscle layers in its wall. Several taxa are characterized by these features (Gibson, 1982a), including *Pseudocarcinonemertes* in the Carcinonemertidae, *Dichonemertes*, *Emplectonema*, *Nemertes* and *Paranemertes* in the Emplectonematidae, *Otonemertes* and *Ototyphlonemertes* in the Ototyphlonemertidae, and *Gononemertes* in the Prosorhochmididae. *Pseudocarcinonemertes*, an ectohabitant on lobsters, differs from *actinophila* in possessing a well developed zone of submuscular glands extending throughout the body length, a short but distinct oesophagus and separate sexes (Fleming and Gibson, 1981), species of the ototyphlonemertid genus possess statocysts in their cerebral ganglia as well as differing in other ways (Kirsteuer, 1977), *Gononemertes* species are dioecious, have an extraordinarily extensive parenchyma and live commensally with ascidians (Gibson, 1974), members of the genera *Dichonemertes*, though hermaphroditic, have their testes located anteriorly close behind the brain whereas the ovaries are situated in the middle and posterior body regions (Coe, 1938) and *Dichonemertes coensis* Friedrich is also ovoviviparous (Friedrich, 1970), *Emplectonema* species possess strongly developed dorsoventral muscles, a distinct oesophagus and a closed pre-cerebral septum (Corrêa, 1955; Friedrich, 1955), one dubious member of the genus, *Emplectonema spongicola* (Bergendal), also being hermaphroditic (Bergendal, 1903), *Nemertes* taxa, with one hermaphroditic representative (*Nemertes hermaphroditicus* Gibson), have an anteriorly divided body wall longitudinal muscle layer, large numbers of eyes and an oesophagus (Kirsteuer, 1974; Gibson, 1982b), and *Paranemertes* species typically possess a divided longitudinal musculature and well developed submuscular glands (Coe, 1905; Kirsteuer, 1974; Gibson, 1982b); further, the blood system of all the above taxa exhibits simple grades of organization quite unlike that occurring in *actinophila*.

Friedrich (1955) was cautious over the generic significance of hermaphroditism, but Corrêa (1966) used the feature in combination with other anatomical characters in her generic diagnosis of *Coenemertes*. In addition to the taxa already discussed, hermaphroditism has been reported for the following marine monostiliferous hoplonemerteans: *Amphinemertes caeca* (Coe), *Poikilonemertes vivipara* Stiasny-Wijnhoff, species of *Prosadenoporus* and *Prosorhochmus*, *Sacconemertella lutulenta* Iwata, *Tetrastemma hermaphroditicum* (Keferstein), *Tetrastemma kefersteinii* (Marion) and *Tetrastemma marionis* Joubin (Coe, 1940; Stiasny-Wijnhoff, 1942; Friedrich, 1955; Corrêa, 1966; Iwata, 1970; Gibson, 1982a; Gibson and Moore, 1985). Differences between the organization of the blood system, rhynchocoel and nervous system of *actinophila* and these taxa, as well as other structures, indicate that the present nemerteans cannot be closely related to any of them. Bürger's species thus does not belong in any of the existing monostiliferous genera and the new genus, *Cryptonemertes*, is accordingly established for it.

### *Cryptonemertes* new genus

*Etymology.*—The generic name, derived from the Greek *kryptos* (hidden), indicates the nemerteans' characteristic habit of living beneath the pedal disc of actiniarians.

*Diagnosis.*—Monostiliferous marine hoplonemerteans; rhynchocoel one quarter or less of body length, with wall containing two distinct muscle layers; proboscis with normal construction and two to four accessory stylet pouches; body wall musculature without diagonal layer, longitudinal fibers reaching to tip of head; no pre-cerebral septum; frontal organ present; cephalic glands extensive, reaching post-cerebrally; cerebral sensory organs small, simple, far anterior to brain, opening ventrolaterally; cerebral ganglia comparatively small, confined to dorsal half of head; lateral nerve cords in foregut region with accessory lateral nerves; foregut opening into rhynchodaeum immediately in front of proboscis insertion, without oesophagus but with regionally differentiated stomach, intestinal caecum short, with lateral but no anterior diverticula; blood system complex, developed into network of interconnected vessels throughout length of body, mid-dorsal blood vessel missing but two vascular plugs developed from posterior extensions of cephalic vessels; parenchyma moderately extensive; excretory system restricted to foregut region, opening via single nephridiopore on each side; hermaphroditic, gonads comprising numerous irregularly distributed ovotestes.

*Type-Species.*—*Cryptonemertes actinophila* (Bürger, 1904). The genus is at present monotypic. *Cryptonemertes actinophila* has so far been recorded in association with the following species of actiniarians: Actiniidae, "*Tealia davisii*" (Bürger, 1904: see footnote 1); Actinostolidae, *Stomphia coccinea* (O. F. Müller) (present paper), *Stomphia didemon* Siebert (present paper) and *Stomphia polaris* (Danielssen) (Bürger, 1904); Hormathiidae, *Allantactis parasitica* Danielssen (Thorsen's Christmas card, 1949).

The nemertean has also been found at the following locations: west side of Bear Island, approximately 74°30'N, 19°00'E; approximately 1 sea-mile (1.85 km) north-east of Ross Island, the northernmost island in the Svalbard group, 80°48'N, 21°00'E; Hinlopen Straits between West Spitsbergen and North East Land, in Lomme Bay, Svalbard, approximately 79°40'N, 19°00'E; middle part of Ice Fjord, West Spitsbergen, Svalbard, approximately 78°20'N, 15°00'E; mid-way between Jena and Abel Islands, Kong Karls Land, Svalbard, approximately 79°00'N, 30°00'E; approximately 11 sea-miles (20.4 km) north-west of Haarfagrehaugen

on Swedish Foreland, Kong Karls Land, Svalbard, 78°45'N, 27°30'E (Burger, 1904); Scoresbysund, East Greenland, approximately 70°25'N, 22°30'W (Thorson's Christmas card, 1949); North Iceland, Eyjafjörður, approximately 66°00'N, 18°30'W (Friedrich, 1958: actiniarian host species not recorded); vicinity of Friday Harbor, San Juan Island, Puget Sound, U.S.A., approximately 48°32'N, 123°00'W; Satellite Channel, off Vancouver Island, Canada, approximately 48°43'N, 123°30'W (present paper).

Bürger (1904) reported that the nemerteans and their hosts were dredged from depths of 0–240 m from coarse gravel covered with balanoid scars, blue mud between fist-sized stones, yellow clay and mud with numerous worm tubes, and stony ground covered with calcareous red algae.

#### IS *CRYPTONEMERTES ACTINOPHILA* A COMMENSAL SPECIES?

Although Bürger's (1904) evidence for commensalism was inadequate, features of the reproductive and blood systems support his hypothesis.

The gonads of monostiliferous hoplonemerteans are typically and primitively confined to the intestinal body regions, where they form two lateral rows in the parenchyma alternating singly or in small groups with the intestinal diverticula. A multiplication in gonad number and concomitant loss in regularity are modifications characteristically associated with taxa known to possess parasitic or commensal habits, such as *Carcinonemertes*, *Gononemertes* and *Pseudocarcinonemertes* (Humes, 1942; Gibson, 1974; Fleming and Gibson, 1981). The entocommensal bdellonemertean genus *Malacobdella* similarly possesses large numbers of irregularly distributed gonads (Gibson, 1968), although in one species, *Malacobdella minuta* Coe, the gonads are relatively large, few in number and arranged in a single irregular row on either side of the body (Coe, 1945). That the gonads in *Cryptonemertes actinophila* are both unusually numerous and irregularly distributed on all the body margins thus tends to suggest that the species may possess a commensal mode of life.

The blood system of *Cryptonemertes actinophila* is complex and extremely well developed. Of particular interest is the extraordinary density of red blood corpuscles. Varndell (1980) showed that in another hoplonemertean, *Amphiporus lactifloreus* (Johnston), the red pigment is haemoglobin and concluded that it served to facilitate diffusion in a manner analogous with vertebrate myoglobin. Varndell also suggested that the cerebral ganglia probably require a constant supply of oxygen whereas the other body tissues conformed to external oxygen levels, which might become very low. Living beneath the pedal discs of actiniarians *Cryptonemertes* will be liable to become covered with mucus, derived both from its own secretions and from those employed for adhesive purposes by the anemones; the tenacious nature of these secretions is illustrated by Bürger's (1904: 58) comment that the nemerteans usually remain attached to the actiniarians even after preservation. Although little is known about nemertean respiratory physiology, it is generally assumed that oxygen uptake occurs across the whole body surface. A thick coating of mucus over the body, therefore, is likely to decrease the availability of oxygen from the environment. In the laboratory *Cryptonemertes* seems to emerge from beneath the pedal disc in response to increased temperature or light (Robson's notes, August 1963), but if it normally spends much of its time hidden below the actiniarians its long-term oxygen requirements may only be satisfied by the development of specialized respiratory arrangements. Anatomical evidence shows that *Cryptonemertes* has an extensive blood system provided with



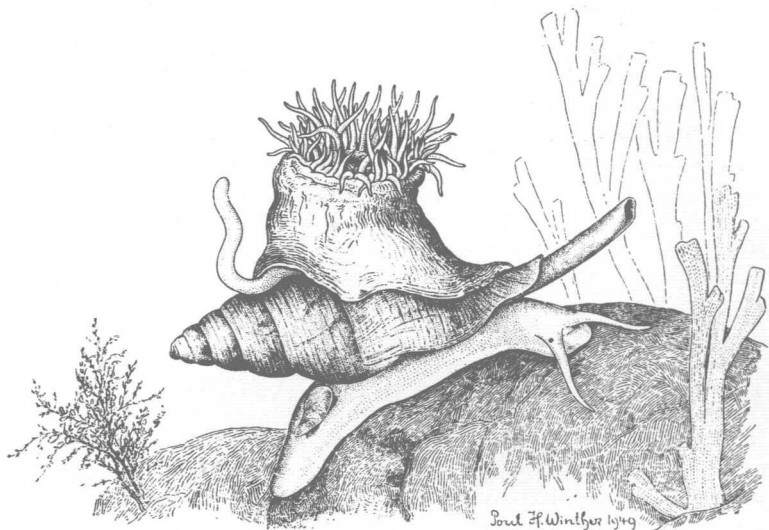


Figure 30. Gunnar Thorson's 1949 Christmas card illustration, drawn by Poul H. Winther, showing a specimen of *Cryptonemertes actinophila* emerging from beneath *Allantactis parasitica* attached to the shell of *Sipho curtus*.

enormous numbers of blood corpuscles containing haemoglobin or some other respiratory pigment.

The organization of the blood and reproductive systems in this species thus provides morphological support for the view that it is a commensal. This evidence is strongly reinforced by behavioral observations noted on a Christmas card produced by Gunnar Thorson in 1949. The card bears an illustration (Fig. 30) with the caption "A gastropod, *Sipho curtus*, with a sea-anemone, *Allantactis parasitica*, on its shell. In more than 20% of the cases examined, the residence of a commensalistic nemertean, *Nemertopsis actinophila*, is found between the shell and the foot disc of the sea-anemone."

"The sea-anemone, though catching and digesting other species of worms, also nemerteans, which happen to touch its tentacles, will, without closing its pharynx or moving its tentacles, allow *Nemertopsis* to enter its gastral cavity, to feed here, and to leave the stomach again with its prey."

Thorson's observations are significant because of the deductions which can be made from them. Like pomacentrid fishes of the genus *Amphiprion*, the nemerteans are evidently protected from the effects of the anemone cnidae. Whether this is because they somehow avoid triggering nematocyst discharge or have some immunity to the anemone toxins is unknown, but the lack of movement evidenced by the anemones may favor the former hypothesis. Also the manner whereby the nemerteans enter the gastric cavity of the anemones in search of food appears to be more than just a casual behavior; possibly the mucus covering the nemerteans' bodies protects them from the digestive effects of the gastric secretions. What the worms are using as food is not known; they may be feeding upon partly digested gastric contents, upon freshly ingested prey, or even upon endodermal tissues of the anemones.

*Cryptonemertes actinophila* is almost invariably found in intimate association with actinarians, shares an identical or closely similar coloration with them (possibly an example of cryptic coloration), and exhibits both morphological and

behavioral features indicative of a true relationship with its host. Bürger's (1904) identification of the species as a commensal is thus vindicated.

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